

Home range and habitat selection of Long-eared Owls (*Asio otus*) in Mediterranean agricultural landscapes (Crete, Greece)

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ABSTRACT

The Long-eared Owl (*Asio otus*) in Crete (Greece) is a common agricultural species affected by the recent changes in agro-forestry systems. Concrete studies of habitat selection are needed in order to improve our knowledge of its foraging behaviour in managed rural landscapes. In the present study, we analysed the home range size and habitat selection of 11 Long-eared Owls inside olive groves in the plain of central Crete using radio tracking data and remote sensing images. Six nominal scale and 11 landscape scale predictors were used for habitat selection analysis, using a maximum entropy approach. Home range size ranged between 337 and 969 ha while a 52% of home range overlap was observed suggesting that Long-eared Owls do not defend hunting territories. At the nominal scale, distance to potential roosts (trees) was the most important contributor to model performance, followed by vegetation heterogeneity. Furthermore, local heterogeneity of greenness was a better predictor than simply greenness at the presence location. At the landscape scale the amount of habitat openness significantly improved model performance. Incorporating landscape heterogeneity improved habitat selection prediction compared to using only discrete land cover classification. Results of our study pinpoint that although Long-eared Owls exhibit a wide range of habitat tolerance, they prefer mixed habitat conditions avoiding particularly open areas or dense olive plantations. The research has implications in the face of new reforms of European Common Agricultural policy which emphasised the importance of landscape structure in preserving biodiversity in agricultural areas of Europe.

Keywords: *Asio otus*, olive groves, home range, habitat selection, Crete

1. INTRODUCTION

Landscape heterogeneity plays a key role on habitat selection of communities of nocturnal predatory birds (e.g. Strøm and Sonerud, 2001; Benton *et al.*, 2003; Moreno-Mateos, *et al.*, 2011; Barbaro *et al.*, 2016) and may influence their predator-prey relationships, their selection of breeding sites and the location of winter roosts (Martínez *et al.*, 2003; Makarova and Sharikov, 2015). For example, it has been shown that natural scrublands and water bodies are crucial for the persistence of nocturnal birds in a Mediterranean agricultural landscape, while roads can negatively affect species such as the Little Owl (*Athene noctua*) and the Eurasian Scops Owl (*Otus scops*) (Moreno-Mateos *et al.*, 2011). Other notable works dealing with habitat preferences suggest that the presence of the Eagle Owl (*Bubo bubo*) is positively related to the preferred habitat of its main prey (Martínez *et al.*, 2003), while the choice of spatial scale may mirror different habitat requirements (Martínez *et al.*, 2003; Martínez and Zuberogoitia, 2004).

The Long-eared Owl (*Asio otus*) is a typical owl of the family Strigidae widely distributed across the Holarctic realm (Snow and Perrins, 1998; Mebs and Scherzinger, 2000; Duncan, 2003). In Europe, the species is mostly sedentary, although birds from central regions migrate south during harsh weather conditions and overwinter in Morocco (Atlas Mountains), the Mediterranean islands, south Turkey, the Levant region and northern Egypt along the river Nile (Saurola, 2002; Michalonek *et al.*, 2004). In Greece, Long-eared Owls breed and overwinter on the mainland as well as on several islands reaching as south as Crete (Handrinos and Akriotis, 1997). Long-eared Owls are observed across a wide altitudinal range, breeding from farmland and lowland oak woods to the upper forest belt in years rich in food availability (Mikkola, 1983; König *et al.*, 1999; Henrioux, 2002). Preferred foraging habitats include woodland and agricultural edges, grass fields, meadows and bogs, but if competition is high, sparse forests are also used for hunting (Galeotti *et al.*, 1997). In winter, large groups of birds may gather at

communal roosts in gardens, parks, or cemeteries and are often associated with food abundance around human settlements and agricultural landscapes (Graig *et al.*, 1985; Snow and Perrins, 1998; Escala *et al.*, 2009; Sharikov *et al.*, 2010; Noland *et al.*, 2013). The species feeds mainly upon small rodents e.g. voles (Arvicolinae) and mice (Murinae) (see Mikkola, 1983 and references therein) although its trophic spectrum varies across latitudes and among seasons showing a great plasticity that contains even carrion (Birrner, 2009; Mori *et al.*, 2014). The species diet shows higher prey diversity in the Mediterranean mixed agricultural areas compared to other European regions confirming its opportunistic strategy towards food selection and suggesting that owls hunt in habitat mosaics (Gryz and Krauze-Gryz, 2015; Rodríguez *et al.*, 2006).

Long-eared Owls have a relatively small body mass (280–350 g) and a wide wing length (≈ 300 mm) resulting in a relatively low wing loading (Cramp and Simmons, 1985). This adaptation reflects their main flight and foraging behaviour, *i.e.* fast wing beats followed by short intervals of gliding and plunging to prey from a perching site respectively (Mikkola, 1983). This flight and hunting pattern indicates that food searching should be conducted most efficiently over relatively open land where ground cover is patchy or sparse (Kavanach, 2002). In this context, a habitat selection study for the species could be based on a multi-scale approach (Johnson, 1980) assuming that birds are able to follow hierarchical decision processes at different scales regarding resource utilisation (O'Neill *et al.*, 1988; Martínez and Zuberogoitia, 2004). Furthermore the perceptual range, defined as the maximum distance from which an animal can perceive the presence of remote landscape elements such as suitable habitat patches within its home range (Zollner, 2000) becomes a crucial issue in defining resource availability and selection (Thomas and Taylor, 2006). Moreover, the species territoriality has been ambiguous as relevant studies suggest small nesting territories and exclusive foraging areas or no territorial hunting grounds at all (Mikkola, 1983; Wijnandts, 1984; Voous, 1988).

Data on the habitat selection and diet composition of Long-eared Owls have been reported from several European regions including the Mediterranean basin where the dominant land cover type was dry arable land or mosaics of several rural land-use types such as cultivations, irrigated crops, tree plantations, orchards, vineyards and rural settlements (Martínez and Zuberogoitia, 2004; Leader *et al.*, 2008; Escala *et al.*, 2009; Bartolommei *et al.*, 2012). In most of the aforementioned studies, significant predictors of site occupancy were open areas, forest edges, patches of arable land and small scale cultivations. A number of studies dealing with their diet and its seasonal composition have shown a high prey species diversity attributed to landscape heterogeneity that provides microhabitats suitable for a large number of prey species, e.g. small mammals and birds (Alivizatos and Goutner, 1999; Alivizatos *et al.*, 2005; Kafkaletou-

Diez *et al.*, 2008; Kontogeorgos, 2011). However specific studies on the species habitat requirements, resource selection strategy, its foraging behaviour and home range size are largely lacking.

In the present study, we focussed on habitat preferences of Long-eared Owls on the island of Crete, which is the southernmost edge of the species' breeding and wintering distribution in Europe and a significant area for overwintering owl populations (Kontogeorgos, 2011). In addition, given that the species occurs in agro-forested systems which are currently under dynamic changes on the island (Papanastasis, 2009), Long-eared Owls are likely to be affected and could be used as a farmland bioindicator species depending on both open rural landscapes for hunting and forest edges and tree stands for nesting and roosting. This is especially so considering that rural areas of Crete are managed semi-extensively and cultivation and farming methods affect the population density and feeding ecology of wintering raptors (Tzortzakaki *et al.*, 2012). Bearing these in mind our aims were: (a) to estimate the home range size of Long-eared Owls in a typical Mediterranean landscape; (b) to investigate the species habitat selection in the dominant rural land cover type of Crete, *i.e.* olive groves; and (c) to identify the habitat requirements of Long-eared Owls in their foraging movements.

2. METHODS

2.1 Study area

The study was conducted in the Mesara area which comprises the biggest alluvial plain on Crete located in the central-southern part of the island (35°2'45"N, 24°56'17"E) covering an area of 112 km² (Figure 1). The plain is elongated with a slope gradient on the east to west axis, reaching the Mediterranean coastline to the west. The climate is typically Mediterranean with long and dry summers and relatively warm and rainy winters. Dryness is very prominent with no rainfall from late spring to early autumn. The mean summer temperature reaches 28 °C and the average winter temperature is around 12 °C (Voudouris *et al.*, 2012). The plain is a semi-intensively managed agricultural area dominated by olive groves, vineyards and citrus plantations. Land ownership is divided into small parcels creating significant heterogeneity within the plain. The study site is located in a lowland agricultural area of olive groves where Long-eared Owls gather at communal roosts during the winter with as many as 60 individuals congregating in a small stand of *ca* 30 mature Calabrian Pines (*Pinus brutia*) and up to 45 individuals roosting together on single trees (Kontogeorgos, 2011). The study mainly covered the species non-breeding period delimited in relation to its tendency to form communal roosts outside the breeding season namely between late August and

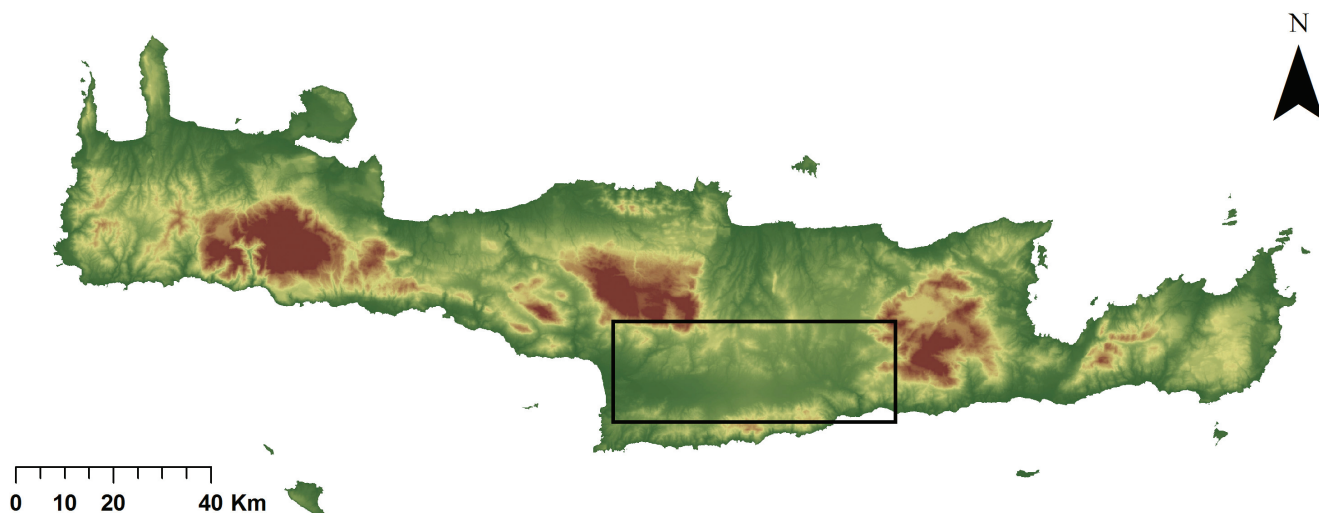


Figure 1 Map of the study area.

early March (Mikkola, 1983; Cramp and Simmons, 1985; Kontogeorgos, 2011; Newton *et al.*, 2002).

2.2 Long-eared Owl data collection

Long-eared Owls were trapped by the aid of mist-nets erected near a communal roost during November–February in 2010 and 2011. Overall, 35 birds were captured, ringed and blood sampled. Thirteen of them were equipped with tail-mount or backpack VHF transmitters weighing 11 g (BioTrack Inc., UK), having a battery-life expectancy of 6–9 months and a detection range of 1–1.5 km in line of sight. Transmitters were sewed and glued on tail feathers or harnessed on the Long-eared Owls by the use of Teflon ribbon (Kenward, 2001). Radio-tagged birds were primarily traced by the aid of an omni-directional whip car antenna and a hand-held receiver (Communication Specialists, USA) and then followed by the peak signal with the aid of a directional three-element Yagi antenna till visual contact was possible ('homing', White and Garrot, 1990; Garton *et al.*, 2001). Owl position was noted on a 1:100,000 scale map. Otherwise, triangulation was pursued (Kenward, 1987; Buehler *et al.*, 1995) acquiring two to three radiolocations per radio-tagged individual (*i.e.* successive GPS fixes plus compass bearings at a time step of ca 15 min). The estimated location of tagged Long-eared Owls was calculated by the use of the LOAS 4.0 software (Ecological Solution Software, 2010) accepting error polygons of up to 0.1 ha. The minimum number of points for home range analysis was set at 15, since sample sizes of 15–20 radiolocations have proved to be adequate for home range estimation (Henrioux, 2000; Lövy and Riegert, 2013). Overall, one radiolocation was pursued per tagged bird each field night, though in some cases a second one was allowed after ca 2.5 h. Radio tracking was initiated shortly after sunset and radio-fixes were acquired on average at 23:26 h (range = 18:00–03:57 h).

2.3 Habitat data collection

Descriptive data regarding land cover were gathered by applying stratified random sampling. In total 300 sites were visited in the wider area of the Long-eared Owl's outermost radiolocations, of which 149 were olive stands. Finally 131 of the 149 olive stands were used for analysis after data exploration for accuracy assessment in relation to ground control points and remote sensing image classification. In each field plot, geographical coordinates were recorded in WGS84 Geographical Coordinate System using a mobile application for Android (Offline Maps); meanwhile aerial photos stored in a handheld smartphone device facilitated visual assessment of positional accuracy in the field. Plot location was adjusted to coincide with the centre of the target land cover class in order to minimise the number of mixed pixels in subsequent image analysis. Seven main land cover types were identified in study plots, *i.e.* (1) olive groves, (2) vineyards, (3) irrigated vegetable fields, (4) annual crop fields (mainly wheat), (5) phrygana, (6) riparian vegetation and (7) settlements or artificial structures (*e.g.* barns, greenhouses *etc.*). Measurements of habitat heterogeneity included understory vegetation (proportion at steps of 10% of ground vegetation visually estimated between four olive trees), soil (proportion of earth on the ground), rock (proportion of rocks on the ground), tree distance (planting distance inside olive groves), irrigation (presence of irrigation pipes – binomial [yes/no]), mean tree height (m), and mean tree crown diameter (m). Tree height and crown diameter were measured for 10 individual trees and summarised into mean values since all olive trees were of the same age (estimated by their trunk diameter). Tree height measurements were taken using TruPulse 360 optical range finder (Laser Technology Inc.) at an accuracy of 0.1 m. As olive trees are planted at regular spacing to aid agricultural works, distance between trees and average crown size were used to estimate canopy

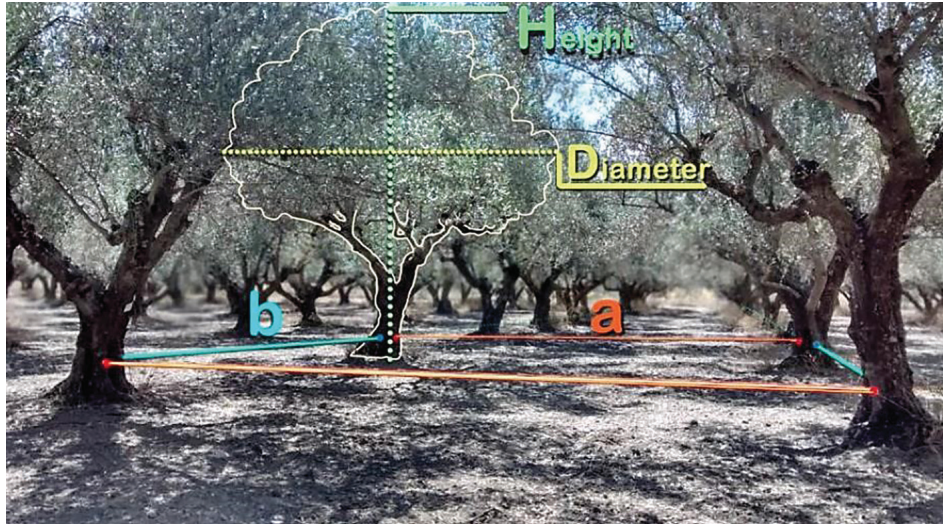


Figure 2 Measurements taken in each olive grove sample plot.

cover. Distance between trees was set as an index of openness (Figure 2). Canopy cover was calculated as the area of the average crown divided by the openness index based on the assumption that the olive tree crown has a relatively circular shape, *i.e.* $C = \pi r^2/ab$ where a and b are the distances of olive tree spacing (Figure 2) in the plantation and r is the crown radius of a model tree in the field plot. Canopy cover was then regressed against the normalised difference vegetation index (NDVI) extracted from satellite imagery.

2.4 Home range analysis

All radiolocations were digitised by a geographic information system (QGIS Development Team, 2014) and were visualised using AniMove (AniMove Team, 2008). Prior to analyses radiolocations were tested for temporal randomness using Ripley's K function modified for one dimension, *i.e.* $K(h) = 1/\lambda \times E \times (N_h)$, where N_h is the number of events within a circle of radius h for a randomly chosen point, E the number of events within distance h and λ the overall intensity of points for each individual. If points were sampled randomly, then the number of observations in any time window should follow the theoretical Poisson distribution with intensity λ equal to overall intensity of relocations. The time frame coincided with the earliest date of observation and ended with the last observation from any individual. Bootstrap randomisation was used to generate 95% confidence intervals for the theoretical K expected under the complete randomness assumption. Under the null hypothesis of randomness the observed $K(h)$ should fall within the randomisation envelope (Baddeley *et al.*, 2014). Home range size was calculated by the 'adehabitat' package for R software (Calenge, 2006; R Core Team, 2008) as the minimum convex polygon (MCP 100%), *i.e.* the area containing all relocations and the 95% kernel density estimator (KDE), namely the probability of finding a Long-eared Owl at any given time that was created by applying a bivariate kernel over the presence points (Worton, 1995).

The smoothing kernel parameter (bandwidth) was calculated using the *ad hoc* reference method $h = \sigma n^{(-1/6)}$, where $\sigma^2 = 0.5 \times [\text{var}(x) + \text{var}(y)]$ (Silverman, 1986). Home range sizes by the two methods were compared by the Mann–Whitney U -test in SPSS 16.0 (SPSS Inc., 2007).

2.5 Habitat selection analysis

A dataset of environmental covariates was used to model the resource selection behaviour of the Long-eared Owl population using the MaxEnt software (Phillips *et al.*, 2006; Phillips and Dudík, 2008) which uses a machine learning method for predicting species distribution (Phillips *et al.* 2004; Elith *et al.*, 2011) based solely on presence data and a set of environmental predictors over a geographical region. Prior to model building, a hypothesis was made that there is an 'optimum perceptual range' of habitat selection for the Long-eared Owl, namely extent of the habitat which is relevant when making decisions for movement. In order to find this optimum, landscape context indices were used by applying a standard deviation filter for a range of window sizes on NDVI autumn image (sdNDVI_a, Table 1) at different spatial scales (Figure 3a). In total, 12 window sizes were used ranging from 5×5 to 27×27 pixels, and a preliminary MaxEnt model was fit on each of the 12 sdNDVI predictors separately (Figure 3b). The preliminary models showed that more distinguishable selection was observed when using a medium spatial scale; sdNDVI_a calculated at a window size of 9×9 pixels produced the highest peak in relative response (Figure 3b). In other words, spatial heterogeneity calculated at this scale explained better Long-eared Owl habitat preference, and thus, sdNDVI_a at this particular window size was used as a predictor in the nominal model in the next step.

After the window size selection, two separate models were built with two groups of predictor variables (Table 1). The first, *i.e.* the nominal scale model, included six variables derived directly from ASTER VNIR images (Advanced Spaceborne Thermal Emission and Reflection Radiometer –

Table 1 Predictors used in the resource selection models (NDVI and sdNDVI are both used for spring and autumn seasons)

Model predictors	Description	Calculation	Minimum information class*
<i>Nominal scale model</i>			
NDVI = (NIR-R)/(NIR+R)	Normalised difference vegetating index, i.e. ratio index of the high reflectance of plant biomass in the near infra-red (NIR) region to the low reflectance in the red (R) region of the electromagnetic spectrum.	Estimated from ASTER satellite images. (Values range from -1 to 1 with higher values indicating more green vegetation.)	15 m ²
sdNDVI = $\sqrt{\frac{1}{n-1} \sum_{i=1}^n (x_i - \bar{x})^2}$	n = size of the window (number of pixels). x _i = NDVI inside the window. x̄ = mean NDVI for the window.	Standard deviation of NDVI calculated for a 'moving window' of 9 × 9 pixel for spring (sdNDVIs) and autumn (sdNDVIa).	135 m ²
DIST_roads	Distance to roads.	Estimated from ASTER satellite images.	15 m ²
DIST_conifers	Distance to conifer trees.	Estimated from ASTER satellite images.	15 m ²
<i>Landscape scale model</i>			
LC	Land cover type classification.	Fieldwork of this study.	Minimum patch size
ELEV	Elevation.	Estimated from an ASTER DEM product.	30 m ²
PLAND = $P_i = \frac{\sum_{j=1}^n a_{ij}}{A} \cdot 100$	Percentages of each land cover type within a 90 m radius around a focal pixel.	P _i = proportion of landscape occupied by class i. a _{ij} = area (m ²) of patch ij. A = total landscape area (m ²).	180 m ²
SHDI = $-\sum_{i=1}^m (P_i * \ln P_i)$	Shannon's diversity index, i.e. P _i – proportion of landscape occupied by patch type (class) i.	The probability of two randomly selected pixels belonging to the same land cover type. The index was calculated from a 'moving window' of 180 × 180 m in size. (Small values represent uniform habitat.)	180 m ²
AI = $\left[\sum_{i=1}^m \left(\frac{g_{ii}}{\max \rightarrow g_{ii}} \right) P_i \right] (100)$	Aggregation index i.e. g _{ii} = number of like adjacencies (joins) between pixels of patch type (class) i based on the single-count method. max → g _{ii} = maximum number of like adjacencies (joins) between pixels of patch type (class) i based on the single-count method. P _i = proportion of landscape comprised of patch type (class) i.	The measurement if same class pixels are aggregated or dispersed inside the study window. (Values of zero when patch types are maximally scattered and 100 when there are aggregated in one single patch.)	180 m ²

*Pixel resolution used in MaxEnt 15 m².

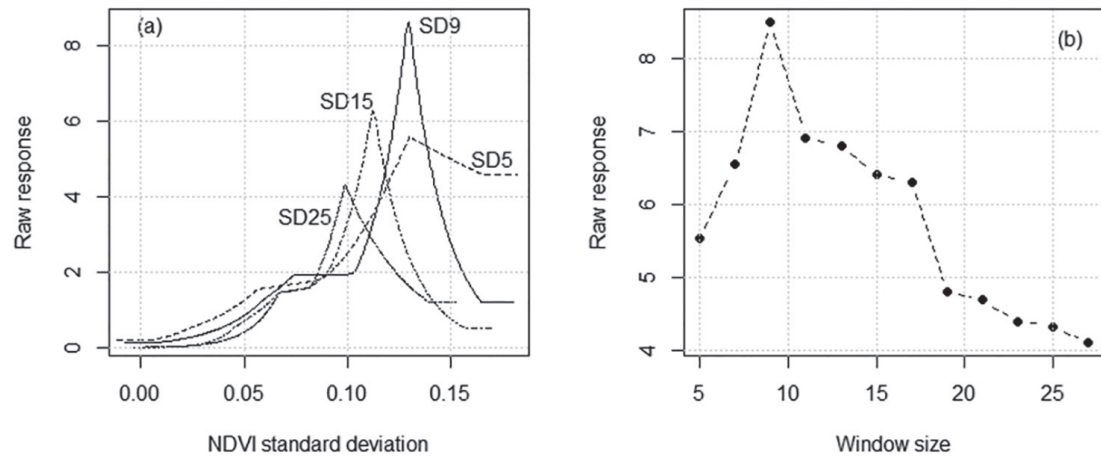


Figure 3 Response curves (a) and maximum (peak) response value (b) from sdNDVIa for different scales. Standard deviation filter was applied over the area at window size from 5 to 27 pixels. Response is unimodal suggesting there is a clear defined preference towards certain spatial context. Raw response is maximised at 9×9 window size.

https://lpdaac.usgs.gov/data_access), using the finest spatial resolution from the ASTER sensor (15 m). The second, *i.e.* the landscape scale model, included 11 variables based on the land type classification acquired by the fieldwork in the sampling plots (Table 1). A land cover map of the study area was derived by combining remote sensing information and fieldwork data and applying parametric classification approach with IDRISI Selva (Eastman, 2012). Measurements of habitat diversity were derived from the land cover map using the software FRAGSTATS by passing a 'moving window' of fixed size assuming that this reflects the scale and manner the Long-eared Owls perceive and responds to their environment (McGarigal *et al.*, 2012). In particular, four heterogeneity indices were set (Table 1). The variability of the NDVI (Jensen, 2005) was used in the nominal scale model, while the percentage of each land cover type (PLAND) surrounding the focal pixel of Long-eared Owl locations, the diversity of habitat types estimated through the Shannon's diversity index (SHDI) (Tuomisto, 2010), and the aggregation index (AI) which measures how compact the land cover types are inside the study plots (He *et al.*, 2000) (Table 1) were used in the landscape scale model. All predictor variables used in the two models were resampled to the pixel resolution of 15 m using the bilinear resampling method in IDRISI Selva (Eastman, 2012).

Model performance statistics were evaluated to choose the appropriate window size for deriving appropriate information hypothesising that higher performance rate (higher raw score) corresponds to the extent of the perceptual range of Long-eared Owls. The extent of the study area was selected in order to include all potentially available sites and was defined as the area around Long-eared Owl locations 2 km from the last observation (namely half the maximum distance between them). A representative sample of 10,000 background points was used to describe the available resource units across the study plots. Given its small size, the number of background points was considered sufficient as a representative estimation of the environmental conditions. Random seed was set to

constant to guarantee that the same set of points is selected for each model, ensuring comparability between results (Lobo *et al.*, 2008; Elith *et al.*, 2011). Both models were built using only hinge features in order to minimise their complexity and facilitate the interpretation of the resulting response patterns (Phillips *et al.*, 2006). Maximising the gain was done until its improvement was below a predefined convergence value or at the 500th iteration. Default convergence threshold of 0.0001 was used. Roughly half of the iterations for both models ended before reaching the maximum iterations limit. Regularisation parameter λ was also set to the default value (Elith *et al.*, 2011). The area under the curve (AUC) of the receiver operating characteristic (ROC) plot was used as a measure of relative model performance (Fielding and Bell, 1997). Mean AUC values after 10-fold cross validation for each model were compared for significant difference using one tailed Student's *t*-test. AUC is one of the available methods for model evaluation and can be used for comparative analysis provided competing models have identical parameterisation (Lobo *et al.*, 2008; Elith *et al.*, 2011) thus in both models the same settings were used. Variable importance was evaluated using both the jackknife and the permutation tests (Phillips *et al.*, 2006) so to investigate how much a specified predictor improves the gain function and how stable it is after randomly excluding data points.

3. RESULTS

3.1 Home range

Overall a total 487 radio-fixes and 279 relocations were obtained ($\bar{x} \pm sd = 25 \pm 9$ radiolocations per tagged Long-eared Owl; range = 15–41) of which 68.8% were acquired during the non-breeding season. Individual birds were tracked for a mean period of 4.7 months ($\bar{x} \pm sd = 143 \pm 78$ days; range = 16–280). Out of the 13 Long-eared Owls, 11 generated a sufficient sample size for home range analysis

(i.e. ≥ 15 points per individual) and five produced an adequate dataset of 171 relocations i.e. $\bar{x} \pm sd = 34 \pm 5$ points per individual (range = 30–41) for the optimum perceptual range estimation (i.e. window size) of habitat selection (Downs, 2008). The monitoring period of the later Long-eared Owl group spanned between 6 to 8 months ($\bar{x} \pm sd = 206 \pm 55$ days; range = 130–280). As home range analysis is sensitive to outliers and study area boundaries, one unusual observation located 15 km to the southeast of the communal roost was rejected. All observations suffered from small scale clustering because of unequal spread of observations across the study period. Nevertheless, at big

window sizes Ripley’s *K* estimate stabilised and fell within 95% bootstrap confidence boundaries. Almost all Long-eared Owls departed from their roost with fast wing beats followed by short intervals of gliding, heading to the olive groves of the surrounding area. However, their main foraging pattern was rather static as they were often traced perching on olive and cypress trees during the night. Home range size based on the MCP method was smaller than the KDE estimate but not significantly so (i.e. $\bar{x}_{MCP100\%} = 373$ ha, range = 47–900 vs $\bar{x}_{KDE95\%} = 969$ ha, range = 152–1770; Mann–Whitney test, $U = 1.04$, $P = 0.29$; Figure 4). The proportional difference in home range size among individuals was higher

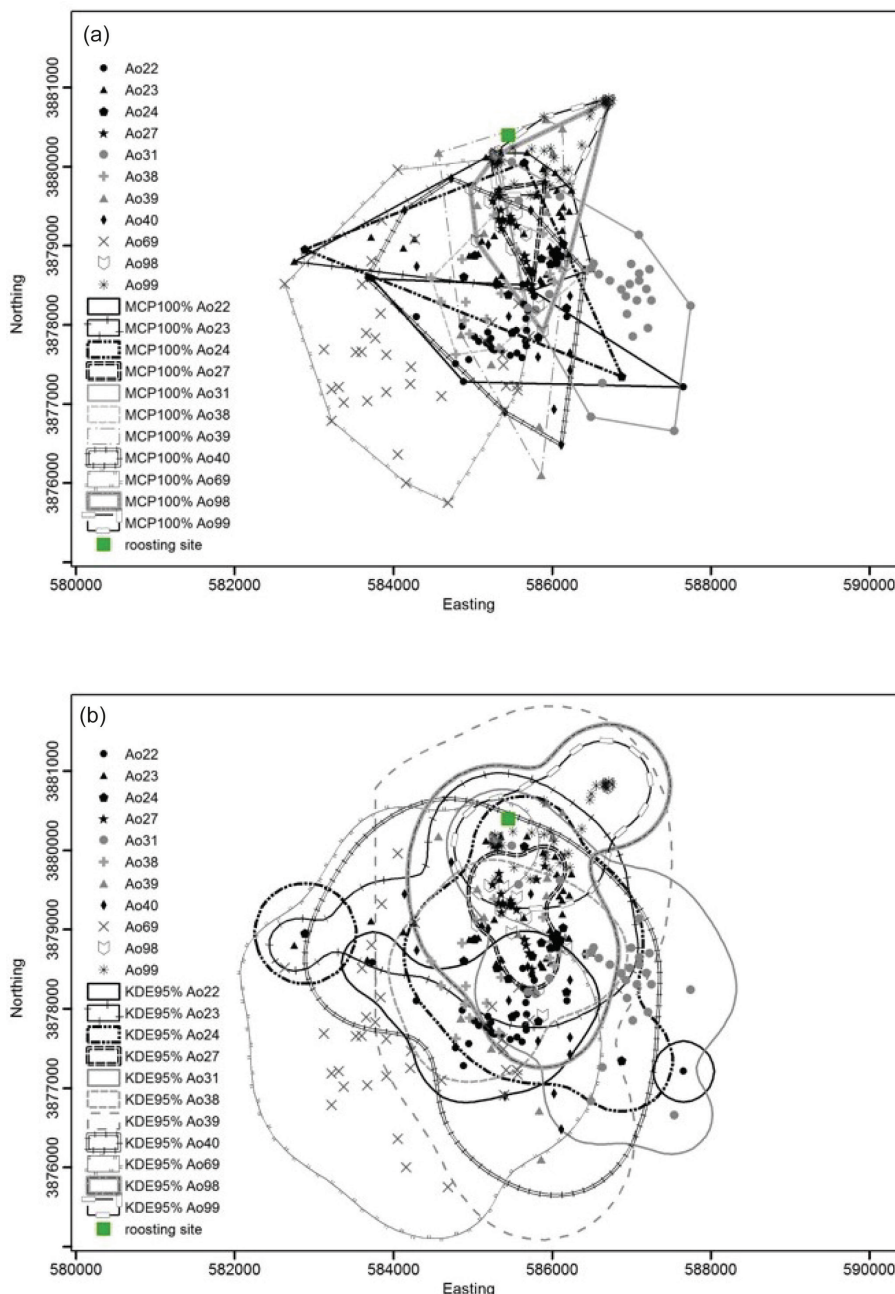


Figure 4 Home range size of Long-eared Owls: (a) minimum convex polygon (MCP100%); (b) kernel density estimator (KDE95%). Horizontal (easting) and vertical (northing) axes are UTM in metres. (The code names AoP22, AoP23, AoP31, AoP69 and AoP99 refer to the ring serial number of each of the five birds.)

when calculated as MCP but individuals' rank was of the same order for 10 out of the 11 individuals in terms of home range size regardless of the method. In addition, a considerable overlap among home ranges was detected (MCP: $\bar{x} \pm sd = 36.5 \pm 27.7\%$, KDE: $\bar{x} \pm sd = 51.7 \pm 28.3\%$; range = 0–100) while theoretically Long-eared Owls foraged at a circular area of a radius ranging from 400 m to 2.4 km from the communal roost (MCP: $\bar{x} \pm sd = 1.1 \pm 0.9$ km, range = 0.4–1.7; KDE: $\bar{x} \pm sd = 1.8 \pm 1.4$ km, range = 0.7–2.4)

3.2 Habitat preference

Both nominal scale and landscape scale models performed well (Figure 5). A one sided Student's *t*-test did not prove significant difference in mean test AUC ($t = 0.61, P = 0.275$). In the nominal scale model, distance to roosting sites and vegetation features were better predictors of the Long-eared Owl's habitat selection behaviour. Their combined contribution was over 90% to model gain (Table 2). A jackknife test showed similar results; gain drop was biggest when distance to conifers was excluded, being also the single most useful variable for maximising model gain (Figure 6). In the landscape scale model, the proportion of open landscape was the most important predictor contributing to more than 40% of model gain. Cumulatively, proportion of land covered by annual crops, elevation and habitat heterogeneity accounted for a total of 73% of the relative contribution. Among the two other landscape measures, *i.e.* diversity and contagion, the former scored higher in terms of contribution to gain function.

In general, Long-eared Owls preferred relatively open areas and avoided human dominated landscapes.

Table 2 Relative contributions of the environmental variables to the MaxEnt models. First estimate (relative contribution) shows the increase in regularised gain contributed by the corresponding variable. For the second estimate (permutation importance) the values of the variables on training presence and background data are randomly permuted and model is re-evaluated. The resulting drop in training AUC is shown in the table, normalised to percentages. Values shown are averages over the 10 replicate runs. (The names of the variables are explained in Table 1. Land cover types used in the Landscape model: PLAND_crop, percentage of annual crop fields [mainly wheat]; PLAND_vine, percentage of annual vineyards; PLAND_vegf, percentage of irrigated vegetable fields; PLAND_resid, percentage of low intensity residential areas; PLAND_olive, percentage of olive groves; PLAND_artificial, percentage of artificial structures [e.g. greenhouses, warehouses etc.]; PLAND_phrygana, percentage of phrygana)

Variable	Relative contribution (%)	Permutation importance (%)
Nominal scale		
DIST_conifers	69.9	62.1
sdNDVIa	20.5	21.8
NDVIs	4.5	7.4
sdNDVIs	3	5.3
DIST_roads	1.5	1.9
NDVIa	0.5	1
Landscape		
PLAND_crop	44.2	23.8
ELEV	21.1	38.8
SHDI	7.8	13
PLAND_vine	7.1	6
PLAND_vegf	6.5	2.2
PLAND_resid	4.9	4.2
LC	2.9	3.1
PLAND_olive	2.6	2
AI	2.3	2
PLAND_artificial	0.4	2.1
PLAND_phrygana	0.2	2.7

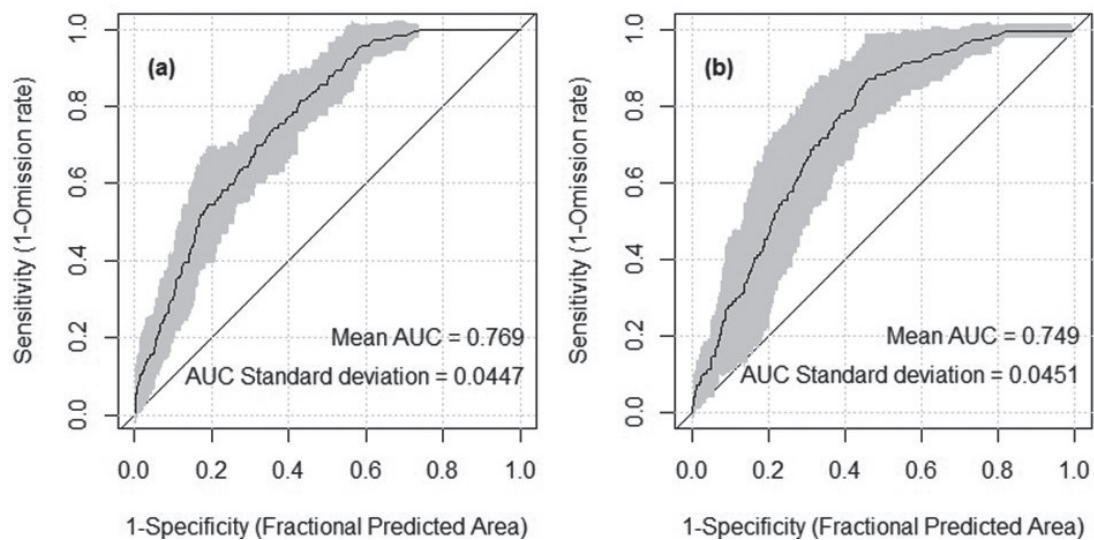


Figure 5 Area under the receiver operating curve (ROC) on test data for the nominal scale (a) and the landscape scale model (b). AUC measures the relative performance of the model. It is interpreted as the probability of a random positive instance being ranked higher than the random background value. Values above 0.5 indicate models that predict better than random.

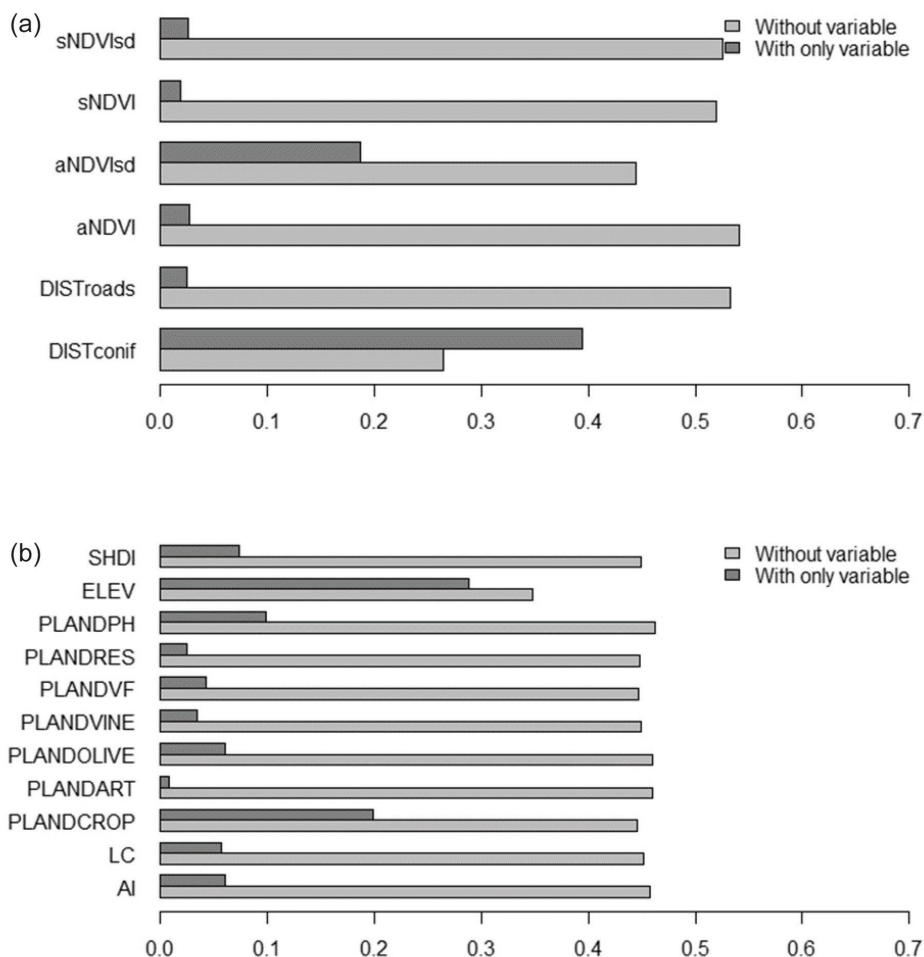


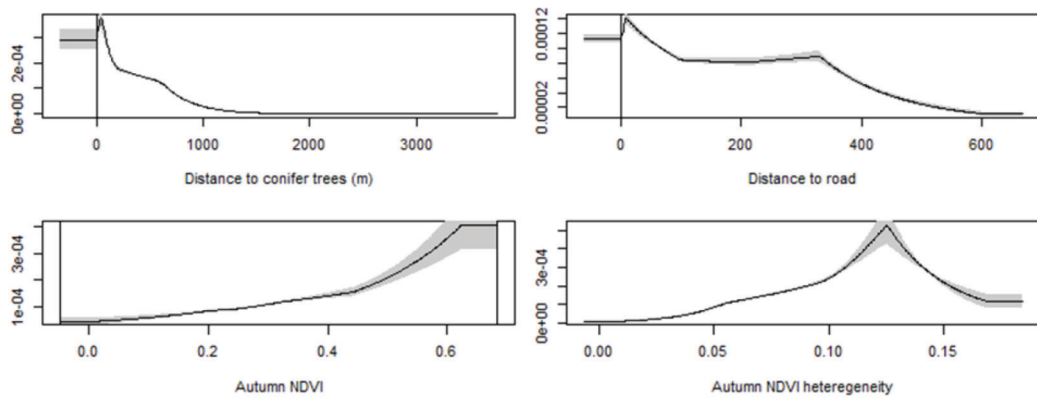
Figure 6 Jackknife test on regularised training gain. Nominal scale model (a) and landscape scale model (b). Model gain is shown as a function of only the variable and when the variable is omitted. The environmental variables with highest gain when used in isolation are DIST_conif and ELEV for both models respectively. They appear to have the most useful information by themselves. The same environmental variables decrease the gain the most when omitted, which therefore suggests that they have the most information that is not present in the other variables. (Variable names are explained in Table 1 and in the legend of Table 2.)

Most response curves were unimodal, exhibiting wide optimum range, or reaching a flat asymptote. In addition, a clear negative correlation to certain environmental conditions was observed. Based on the nominal scale model, Long-eared Owls were more attracted to greener patches inside relatively heterogeneous areas (Figure 7a) with a positive response towards the level of greenness (NDVI) and unimodal response towards vegetation variability (sdNDVI) in the immediate surroundings (Figure 7a). High autumn greenness was mostly related to vegetable fields or vineyards, while high standard deviation values were observed along the edges between different vegetation types. Heterogeneity of greenness was a better predictor than simply greenness at presence locations. The wide plateau of response curve towards the proportion of cropland in the immediate perceptual range indicated a wide tolerance to the extent of open habitats (Figure 7b). Similarly, relative habitat selection towards the proportion of olive groves rose until an optimum of about 75% of the local area. In fact, these

two habitats were the most common land cover types in the study area, and there is a negative relationship between their proportions (*i.e.* more open areas means less olive plantations).

Shannon's index and the aggregation index were significantly correlated, but because they have different interpretations both of them were kept in the model. Long-eared Owls showed a different response pattern towards the two indices, suggesting they felt comfortable inside a wide landscape diversity range; most suitable at the intermediate values of SHDI (Figure 7b). On the other hand, response toward the level of aggregation of same class pixels (AI) had a clear unimodal shape rising steadily towards optimum around 80% (Figure 7b). A linear negative response was observed towards the proportion of human landscapes (artificial and residential areas) and phrygana (Figure 7b). A higher proportion of these types of landscape was unfavourable for the Long-eared Owls. When the entire model was taken into account, these three predictors were complementing

(a)



(b)

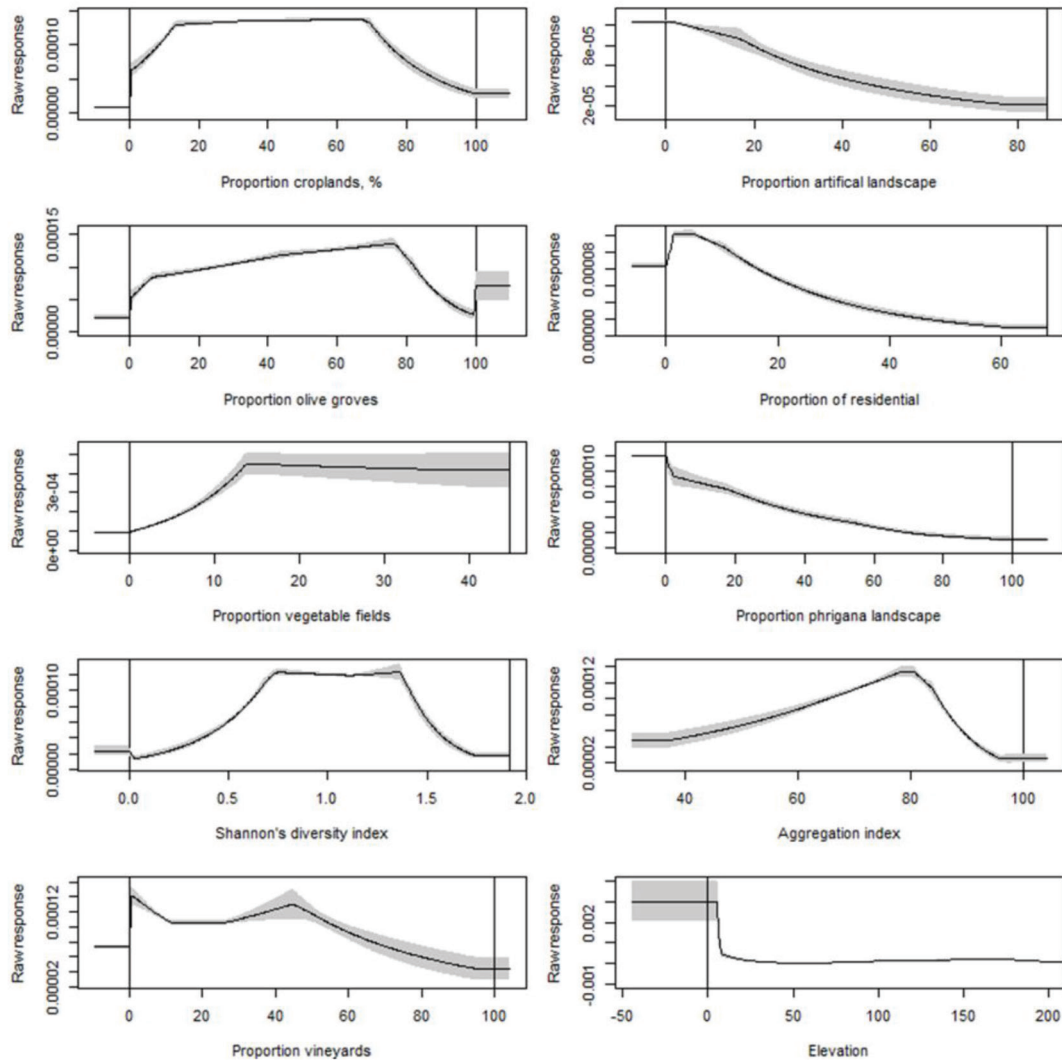


Figure 7 Response curves for (a) the nominal scale model (b) the landscape scale model. (The curves refer to the model built with each of the variables separately.)

each other and therefore redundant. Variables with no explanatory power (because the variation was already explained by other variables) had flat response curves in the final model.

4. DISCUSSION

The species hunting behaviour observed in the present study was consistent with the findings of other researchers (Wijnadts, 1984; Galeotti *et al.*, 1997; Henrioux, 2000), although hunting in flight (Voous, 1988) cannot be ruled out as a hunting technique. Untagged birds were recorded to flap low over the ground or hover over open fields near human settlements where light conditions were better compared to those inside olive groves. The great overlap in the home range of all individuals suggests a lack of territorial behaviour although common foraging might be a by-product of communal roosting (Wijnadts, 1984; Galeotti *et al.*, 1997). However, in several instances, Long-eared Owls radio-tracked during the same night followed different directions after leaving the roost implying that some small-scale spatial separation might occur, although this was difficult to detect. Our findings agree with previous works showing that social behaviour is common in food rich areas where conspecifics share common foraging grounds and defend only a small area around their nest sites, while territorial behaviour is exhibited when food resources are scarce (Glutz von Blotzheim and Bauer, 1980; Weber *et al.*, 2002).

The mean home range size of the Long-eared Owls in Crete was comparable to the range sizes reported by other authors, irrespective of the period examined, *i.e.* wintering or breeding season (Wijnadts, 1984; Graig *et al.*, 1988; Galeotti *et al.*, 1997; Henrioux, 2000; Lövy and Riegert, 2013). However, as the majority of data in this study were acquired during winter months and none of the tagged individuals were found to be nesting, present results should be regarded as more informative for the species non-breeding period. The species hunting area covered ca 650 ha, thus birds forage at a theoretical radius of 1.5 km from their roost or nest. Home range depends on food resources (Newton, 2002), although vegetation structure might be more important for the selection of foraging sites than just prey density (Auschwanden *et al.*, 2005). For this reason the species avoids uniform habitats like open treeless fields preferring a 'network of habitats' with hedges, edgebanks and treelines (Sonneber and Powers, 1976; Mikkola, 1983; Graig *et al.*, 1988; Marks *et al.*, 1994; Galeotti *et al.*, 1997; Henrioux, 2000).

Overall, animals select habitats in order to maximise their fitness and survival (Pyke, 1984). Perceptual range defines the radius window at which animal movement decisions are predictable and has a strong application in landscape connectivity studies (Olden *et al.*, 2004). In this study, locations outside the estimated home range of the owls were considered in order to include a broader

resource availability area. Although other studies usually focus on the landscape structure inside an arbitrary defined circle (Martínez and Zuberogoitia, 2004) or the average flying distance (Bartolommei *et al.*, 2012), here a simple data driven approach was used in order to infer the best window size at which contextual information was relevant to the Long-eared Owl's selection behaviour. The distribution and size of habitat patches is of great significance in habitat selection studies for this species, whereas the number and extent of suitable land cover patches might determine space and habitat use (Henrioux, 2000).

The outcome of the nominal scale model confirmed the importance of preserving specific landscape features. It was shown that sites closer to coniferous trees (or at least large trees) were more likely to be visited by the Long-eared Owls in contrast to patches located far from potential roosts. Our results are in agreement with those of Martínez and Zuberogoitia (2004), who showed that the Long-eared Owl has a higher probability of occupying a territory when the amount of forest around the nest increases at the nest-site and home-range scales. Ideally, other characteristics such as the size and the number of tree stands could be used in marked point pattern analysis to better understand the relationship between hunting behaviour and roost site availability. It is also highly probable that individuals select foraging patches with trees in order to minimise the cost for traversing from roost to hunting grounds as flight is a significant part of the species energy budget (Wijnadts, 1984). Under such hypothesis, relatively less prey-rich but closer patches with trees or with easy-to-catch prey are more likely to be visited as opposed to rich but distant hunting grounds. However, to answer this question, further research should focus on analysing the richness and spatial distribution of the small mammals in relation to the rural management practices in the plain. Small mammal population density in combination with information on roosting trees could be used as a predictor surface for the better understanding of the Long-eared Owl movements and resource selection in spatially explicit models (Manly *et al.*, 1993). The Long-eared Owls visited habitat patches with high green biomass (NDVI values); the NDVI standard deviation which should be used as a landscape heterogeneity index (Riera *et al.*, 1998) for both research and management applications, proved to be significant. In particular, it showed that at a fine scale the level of heterogeneity surrounding foraging sites should be considered when analysing habitat selection data. Indeed, for nocturnal birds such as the Long-eared Owl, the presence of green patches of natural and semi-natural vegetation in an agricultural landscape is positive (Moreno-Mateos *et al.*, 2011).

Similarly the results of the landscape scale model confirmed that the Long-eared Owl is a generalist species tolerating a diverse range of habitat conditions although its diet might be quite restricted to a small number of

prey species (Sergio *et al.*, 2008). The difference in the order of variable importance after randomly permuting data suggested that the land cover scale model was more unstable than the nominal scale model mainly due to the correlation between predictors. This is true because proportion of land cover types are inherently correlated (*i.e.* an increase in the proportion of one land cover class will result in lowering the proportion of other classes). The Long-eared Owls were constrained mainly to the low elevation agro-environmental patchwork covered by olive groves and croplands; the latter being largely dominated by wheat fields which host high densities of their main prey species (Kontogeorgos, 2011). Furthermore, they preferred relatively open areas and avoided human dominated landscapes, although other studies indicate that the species might prefer the proximity of villages (Martínez and Zuberogitia, 2004). The wide selection optimum towards the proportion of croplands suggests that birds are tolerant to changing levels of habitat openness, which is in line with other fine scale studies where the probability of occurrence increases with the degree of open habitats (Martínez and Zuberogitia, 2004; Bartolommei *et al.*, 2012). Strong contribution of elevation to model gain could be attributed to the wide range of elevation included in the analysis and the fact that almost all observations were inside the lowland agricultural area. The strong preference towards lower altitudes was probably related to the species preference to the agricultural matrix rather than the elevation itself. High elevations were not favourable mainly because of the dominance of phrygana, the restricted extent of the olive groves and the pasturelands. Again, this might be related either to the increased food availability of the olive groves and the pasturelands in comparison to phrygana and the proximity to the roosting site, *i.e.* phrygana are further away with no trees to act as perching sites for hunting. The relative predictor contribution indicates that the landscape context is more important than discrete land cover classes. At such fine spatial scale using only visited land cover types to study habitat selection can yield biased results. Birds can easily traverse long distances and, unless very fine temporal data is available to quantify time spent in each habitat type, radio-telemetry studies using compositional analysis (Aebischer *et al.*, 1993) or any other discrete choice model face errors due to timing of observation. Future research on habitat selection should focus on ensuring representativeness of animal space use data (*e.g.* time spent inside habitat type) (Buskirk and Millspaugh, 2006). With high temporal resolution data, new models based on random walk could significantly improve our knowledge on habitat preference and actual habitat utilisation (Börger *et al.*, 2008).

Under low energy budget constraints, animals will focus on minimising the cost for long distance flight, selecting habitat patches closer to the roost tree. In this research, we showed that Long-eared Owls were attracted primarily to relatively heterogeneous areas, staying close

to potential roost sites, and preferring at least some degree of habitat openness. We also showed that studying habitat preference at a fine scale should consider information on landscape context instead of only visited land cover types. Complex landscape structure is common for the Mediterranean islands being a product from century long interaction between nature and humans (Rackham and Moody, 1996). In order to preserve the unique diversity of the area, management should take a holistic view considering the temporal and spatial complexity of the system, and promote practices which enhance the resilience of the agricultural systems. Management and conservation policies focussed on non-interference should thus lead to loss of land use heterogeneity which is an important component for total diversity in the region (Lucio and Atauri, 2001). Instead, stimulating organic farming, and protection and restoration of landscape, forming elements such as conifer tree stands under the new agro-environmental schemes should promote more diverse habitat in the area which will benefit the Long-eared Owls in the region. The aim of the reformed European Common Agricultural Policy (CAP) is to use *in situ* research and monitoring schemes to receive feedback on the effectiveness of new measures (European Commission, 2010). Therefore, long term monitoring of population dynamics of focal species such as the Long-eared Owl can yield a good estimate of the effectiveness of the EU agro-environmental policy and guide further improvements and conservation measures. Monitoring will be further aided by remote sensing data (García Torres *et al.*, 2008). High resolution layers (HRL) would be particularly valuable in home range and landscape scale studies. Together with improved GPS tracking technologies and new development in habitat selection research, they would facilitate development of individual based habitat suitability models. This will further increase our understanding about animal–environmental interactions and help mitigate human impact on natural ecosystems and rural landscapes.

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